

MORPHOLOGY AND RELATIONSHIPS OF THE UPPER CARBONIFEROUS AĪSTOPOD AMPHIBIAN *OPHIDERPETON NANUM*

by M. J. BOYD

ABSTRACT. The holotype and only recorded specimen of the Carboniferous aĭstopod amphibian *Ophiderpeton nanum* Hancock and Atthey 1868 is described in detail and figured for the first time. The vertebrae, ribs, dermal squamation, and premaxilla are characteristic of *Ophiderpeton* and confirm that *O. nanum* is a member of that genus. The relationship of *O. nanum* to other described *Ophiderpeton* species is obscured by the absence of most of the skull in the holotype and by the apparently sub-adult nature of the specimen. The ventral osteoderms are, however, unusually filamentous for *Ophiderpeton* and it is suggested that *O. nanum* be retained as a distinct species, pending revision of the Ophiderpetonidae. A small isolated bone in the holotype may be an interclavicle, suggesting the retention of a vestigial pectoral girdle in ophiderpetontid aĭstopods.

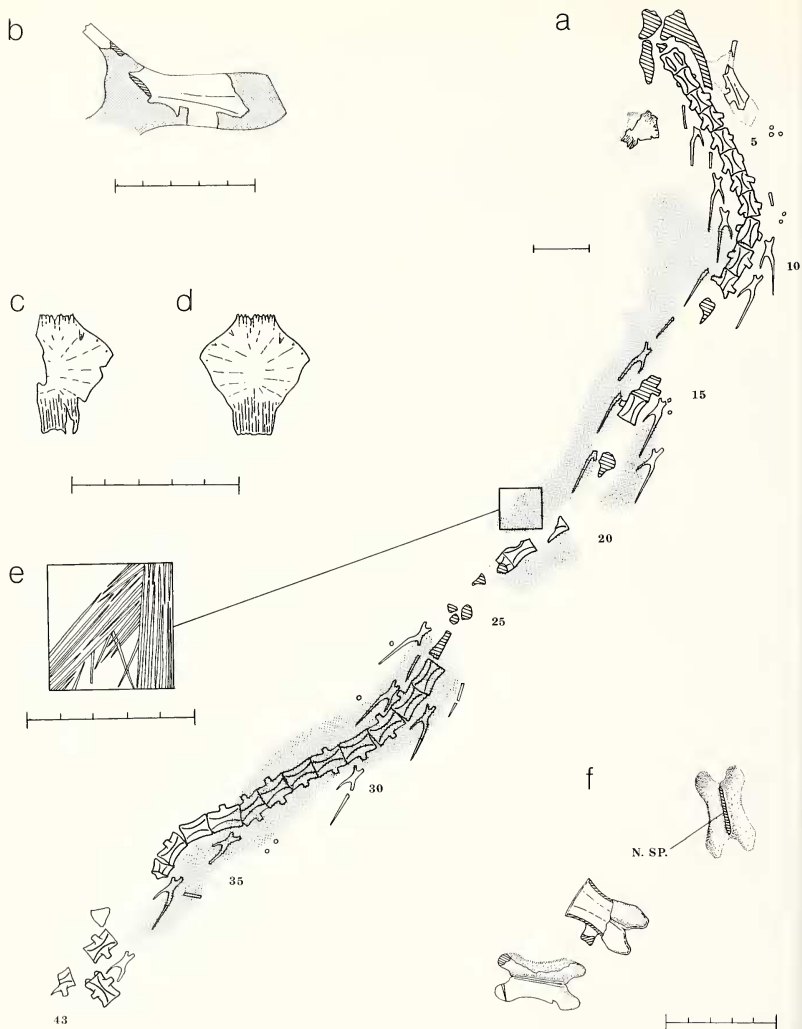
OPHIDERPETON NANUM Hancock and Atthey 1868, is a small 'lepospondyl' amphibian of the order Aĭstopoda from the Upper Carboniferous of Great Britain. The holotype and only described specimen of *Ophiderpeton nanum* was collected around the middle of the nineteenth century and is from the black shale immediately overlying the Low Main coal seam at Newsham, near Blyth, in Northumberland. This horizon lies within the Upper Modiolaris zone of the Middle Coal Measures (Land 1974) and is Westphalian B in age. *O. nanum* forms part of a large and well-known amphibian assemblage from Newsham, whose other members (listed by Land 1974, p. 61) include eogyrinid embolomeres, loxommatid temnospondyls, and keraterpetontid nectrideans. The above taxa appear to be characteristic of Upper Carboniferous coal-swamp lake environments (Milner 1978).

Although *O. nanum* was one of the first aĭstopods to be described, no detailed account of the structure or relationships of this species has hitherto been published and the holotype specimen has never been figured. Neither the original, necessarily superficial, description of *O. nanum* by Hancock and Atthey (1868) nor a subsequent brief account given by Steen (1938), are detailed enough to allow adequate comparison of this form with other described aĭstopods. The present paper is intended to remedy this deficiency.

The holotype of *O. nanum* consists of an incomplete skull and anterior postcranial skeleton preserved in counterpart on two small slabs of shale. The two halves of the specimen are registered in the collections of the Hancock Museum, Newcastle upon Tyne, as G25.34 and G25.35. Because of the small size and fragile nature of the holotype, the only preparation attempted has been the removal of small quantities of matrix from the immediate vicinity of the skull by means of mounted needles.

DESCRIPTION

The skull and most of the preserved postcranial skeleton are situated on slab G25.34 (text-fig. 1*a*). Slab G25.35, henceforth referred to as the counterpart, bears impressions of all but the most anterior seven vertebrae of G25.34, in addition to a small number of actual ribs and isolated patches of the ventral squamation. At some point in the past, small areas of the surface of slab G25.34, bearing sections of vertebral column and associated structures, have flaked away and been lost. However, as the resultant gaps in the vertebral series are all posterior to the seventh vertebra, the number of vertebrae originally preserved may be estimated by reference to the unbroken series of impressions on the counterpart. The skull and skeleton of G25.34 are preserved



TEXT-FIG. 1. *Ophiderpeton namum* H & A. *a-c*, Hancock Museum specimen G25.34: *a*, semi-diagrammatic representation of specimen as preserved. Stippling indicates extent of ventral squamation; *b*, isolated (?) skull element. Stippling represents area preserved as impression only; *c*, interclavicle as preserved; *d*, interclavicle restored; *e*, detail of ventral squamation. *f*, Hancock Museum G25.35. Three isolated vertebrae as preserved. All scale lines represent 5 mm. N.SP., neural spine.

with their ventral surfaces uppermost. A large number of ribs is present. Although most of the vertebrae and ribs are overlain by a thin 'mat' of closely packed, filamentous gastralia, this is often so closely applied that the contours of the structures which it conceals may be clearly seen.

Skull

The skull apparently became disarticulated and scattered prior to preservation and is largely absent. Three distinct masses of poorly preserved bone lie immediately anterior to the first preserved vertebra. It is possible that they represent elements of the palate or neurocranium. A slight depression in the matrix anterior to these may mark the site of the isolated premaxilla noted by Steen (1938, p. 223). No trace of the bone itself remains; it has presumably become detached from the slab and lost.

A relatively large isolated bone, situated to the right of the most anterior four vertebrae in text-figure 1a, may, doubtfully, also belong to the dermal skull. Although much of the bone itself has been lost, the clear impression remaining in the matrix allows no question as to its original form. Its identity, however, is obscure. The element (text-fig. 1b) does not appear to correspond to any bone known in the skulls of either *Ophiderpeton* (A. C. Milner, pers. comm.) or phlegethontiid aistopods (e.g. Gregory 1948; McGinnis 1967). The triradiate form of the element makes it unlikely that it represents part of the dermal pectoral girdle. Possibly the bone in question does not, in fact, pertain to *O. nanum*.

A second isolated element, lying to the left of the vertebral column at the level of the third and fourth vertebrae (text-fig. 1a), is of some interest. Approximately one-quarter of the bone is missing but it is clear that the complete element was of roughly rhomboidal shape (text-fig. 1c-d). It is suggested that this element represents a displaced interclavicle. This hypothesis receives support from the presence of a slight (?parasternal) process at one angle of the bone and the fact that the margin of the element directly opposite the above process is noticeably fimbriated. Interclavicles with fimbriated anterior margins have been described in a number of both 'labyrinthodont' (e.g. Milner 1980, fig. 5) and 'lepospondyl' (e.g. Carroll and Gaskill 1978, fig. 120G) amphibians. No clearly defined ornament or areas for clavicular overlap are visible on the suggested interclavicle but it is possibly preserved with its dorsal surface uppermost.

Vertebrae

Although several vertebrae have been lost from the articulated series of G25.34 (text-fig. 1a), it is apparent from the impressions on the counterpart that the first forty-three vertebrae were originally present. The presence of a single median ventral ridge in all the vertebrae preserved indicates that all are precaudal; the centra of aistopod caudal vertebrae are characterized by a pair of hypapophyseal flanges demarcating the haemal canal (e.g. Zidek and Baird 1978). The vertebrae exhibit a gradual increase in size from anterior to posterior of the series, the most anterior centra measuring 2 mm in length and the most posterior approximately 3 mm. Well-developed parapophyses are borne by all but the most anterior two vertebrae, in which they are represented only by scarcely perceptible lateral projections from the centrum. In vertebrae 3-10 the parapophyses, as preserved, have a posterolateral orientation. In the remaining vertebrae (11-43) they project laterally. In the absence of any indication of the original position of the pectoral girdle it is impossible to determine how many of the vertebrae are cervicals. However, Baird (1964) has noted that the parapophyses of aistopod dorsal vertebrae change their orientation from posterolateral to lateral to anterolateral, from anterior to posterior of the column. It may therefore be concluded that, with the exception of an unknown number of cervicals, the vertebrae of G25.34 are all anterior- or mid-dorsal in position. The vertebral count in an entire specimen of *O. nanum* is unknown. However, a figure of 100+ has been given by Baird (1964, p. 6) for a juvenile of *O. granulosum* Fritsch.

The structure of a typical mid-dorsal vertebra of *O. nanum* will be apparent from text-fig. 2b-d. The centrum is holospondylous and probably deeply amphicoelous. The latter is the aistopod condition and is suggested in G25.34 by the high degree of compression undergone by most centra. Ventrally, the centrum bears a median ridge running the length of the element and broadening at its anterior and posterior ends. The ventral ridge, which appears to have been mistaken for a low neural spine by Hancock and Atthey (1868, p. 277), is flanked by a pair of elongate depressions. The parapophyses are dorsoventrally compressed structures, slightly expanded distally, and have their origins low on the lateral surface of the centrum at approximately the mid-point of its length. None of the vertebrae shows any evidence of the presence of basapophyseal processes.

The vertebrae of G25.34 are preserved with only their ventral surfaces exposed and yield no information on the structure of the neural arch. However, the counterpart slab bears, in addition to impressions of most of the vertebrae of G25.34, three isolated vertebrae from a more posterior region of the trunk (text-fig. 1f). Each of the three is incomplete but together they allow a restoration of most of the neural arch. Two are

almost entire vertebrae with their dorsal surfaces exposed, and the third is a very clear impression of the dorsal surface of the neural arch with the neural spine itself remaining in position. The neural arch is a long and low structure extending the full length of the centrum; whether the two are fused or merely sutured together cannot be determined. The neural spine is very weakly developed and forms a low and narrow ridge running the length of the, otherwise almost horizontal, dorsal surface of the neural arch. The zygapophyses are widely spaced and possess horizontally orientated articular surfaces. Unfortunately, the nature of the available material makes it impossible to determine whether the neural arch is pierced laterally by foramina for the spinal nerves, as is known to be the case in *Phlegethontia* (McGinnis 1967) and at least one *Ophiderpeton* species (Baird 1964).

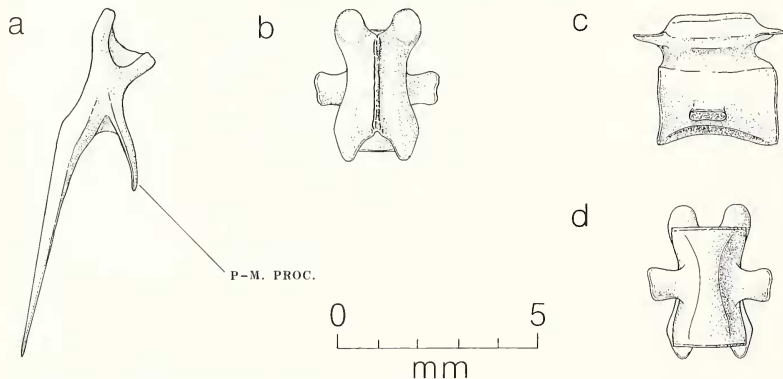
Ribs

Numerous ribs are preserved along the length of vertebral column of G25.34 (text-fig. 1a). Almost all are incomplete and most are at least partially obscured by overlying areas of the ventral squamation. However, a composite restoration of rib structure in *O. nanum* may be made with confidence. Free ribs appear to have been borne by all but the most anterior two of the forty-three vertebrae originally present. The first two vertebrae are also known to be without free ribs in *Phlegethontia* (McGinnis 1967). There is no apparent variation in rib form within the preserved series. The ribs do, however, show a slight increase in size from anterior to posterior.

The structure of a typical precaudal rib of *O. nanum* is depicted in text-fig. 2a. The rib is tetradactyl, in the manner characteristic of the Aïstopoda (Baird 1964). The capitulum is short and stout, and appears to possess a slightly recessed head for articulation with the parapophysis of the vertebra. In all ribs in which it is preserved, the costal process is approximately twice the length of the capitulum and is connected to the latter for most of its length by a thin 'web' of bone. Whether the head of the costal process was recessed, as has been stated to be the case in *Ophiderpeton* by Baird (1964, p. 7), cannot be determined. The shaft, which contributes about two-thirds of the over-all length of the rib, is a robust, stiletto-like structure which tapers distally to a fine point. A well-developed posteromedial process is present. In most of the preserved ribs the posteromedial process exhibits a slight lateral curvature, towards the medial side of the shaft.

Scales

A well-developed ventral squamation is present and, as preserved, takes the form of a 'mat' of closely packed gastralia extending from the tenth vertebra to the forty-third (text-fig. 1a). The squamation has been displaced



TEXT-FIG. 2. Restoration of mid-dorsal vertebra and rib of *Ophiderpeton nanum* H & A. a, rib of left side in dorsal view; b-d, vertebra in b, dorsal view; c, left lateral view and d, ventral view. P-M. PROC., posteromedial process.

to one side of the vertebral column in the anterior part of the trunk, but more posteriorly it overlies the vertebrae and ribs. The individual gastralia are extremely elongate, almost filamentous, structures (text-fig. 1e). In their form they somewhat resemble the hair-like gastralia of the phlegethontiid *Aornerpeton mazouense* (Gregory) (Gregory 1948; Lund 1978), but their tightly packed arrangement and their extent beyond the anterior thoracic region are characteristic of *Ophiderpeton* (Baird 1964). As preserved, the orientation of the gastralia is very variable and Hancock and Atthey (1868, p. 277) suggested that the scales originally lay with their long axes at 90° to the vertebral column. It would seem more likely, however, they were originally arranged *en chevron*, as in many other Palaeozoic amphibians. Such an arrangement is still preserved in some areas of the ventral squamation. The absence of ventral osteoderms in the 'cervical' region and beneath the most anterior dorsal vertebrae is of some interest and may indicate, as Steen (1938, pp. 223, 224) suggested, that the specimen is a sub-adult individual.

Although not altogether absent, as had previously been thought (Steen 1938), the dorsal squamation is represented in G25.34 only by a small number of rounded, pebble-like osteoderms scattered at intervals along the length of the vertebral column (text-fig. 1a). The dorsal squamation of *Ophiderpeton* species usually consists of numerous such scales covering the dorsal and lateral surfaces of the trunk region and tail (Baird 1964). Its almost complete absence in the holotype of *O. nanum* may, like the restricted ventral squamation, indicate that the specimen is a juvenile animal. Such an assumption also offers an explanation of the ready dissociation of the skull elements subsequent to the death of the animal.

DISCUSSION

Despite the incompleteness of the only available specimen of *O. nanum*, it is apparent that this species is a member of the family Ophiderpetontidae, as defined by Baird (1964). Reference to the Ophiderpetontidae is suggested by the following characters of the holotype:

1. The structure of the ribs, in which the shaft is stout and stiletto-like and a well-developed posteromedial process present. In the phlegethontiids *Phlegethontia* and *Aornerpeton* the shaft is usually slender and flexible and the posteromedial process weakly developed or absent (Baird 1964; Lund 1978).
2. The presence of a well-developed ventral squamation composed of numerous, closely packed gastralia forming a continuous plastron. The phlegethontiid ventral squamation consists of a series of widely spaced, filamentous gastralia restricted to the anterior trunk region (e.g. Gregory 1948, pl. 1, fig. 4).
3. The apparent presence of an, at least partial, dorsal or lateral squamation of pebble-shaped osteoderms; no dorsal and lateral armour is known to occur in the Phlegethontiidae (Baird 1964).
4. The form of the premaxilla, now lost, described by Steen (1938, p. 223). This was stated exactly to resemble the premaxilla of *O. amphiuminum*, described by Steen in 1931 (fig. 17B-C). The premaxilla of *O. amphiuminum* and other *Ophiderpeton* species differs markedly from that of *Phlegethontia* in possessing an anterior ascending process (McGinnis 1967, p. 38).

As presently constituted, the Ophiderpetontidae contains only the type genus, *Ophiderpeton* Huxley 1867, and *Coloraderpeton* Vaughn 1969. The latter is a monotypic genus, established by Vaughn (1969) for a number of vertebrae, ventral osteoderms, and an attributed rib from the Upper Pennsylvanian of the Sangre de Cristo Formation in central Colorado. The vertebrae of *Coloraderpeton* are distinguished from those of both *Ophiderpeton* and *Phlegethontia* principally by the form of the neural spine. This, although relatively somewhat higher than in the last two genera, is restricted in its anterior-posterior extent to the middle one-third of the neural arch and possesses a crenulated dorsal edge. The dorsal vertebrae otherwise appear typically aistopod and possess foramina for exit of the spinal nerves. *Coloraderpeton* was placed in the Ophiderpetontidae by Vaughn on the basis of the form of the rib, which has a stout shaft and apparently also a posteromedial process, and of the closely packed, fusiform ventral osteoderms. It is clear from the structure of the vertebrae that the holotype specimen of *O. nanum* cannot be placed in the genus *Coloraderpeton*. On the other hand, the similarity of the ribs, vertebrae, and ventral squamation to those of other described *Ophiderpeton* species appears to confirm the correctness of Hancock and Atthey's (1868) reference of the Newsham aistopod to this genus.

O. nanum was distinguished by Hancock and Atthey (1868) from the only previously described *Ophiderpeton* species, *O. brownriggii* Huxley 1867, by its relatively small size and the almost filamentous nature of the ventral osteoderms. The former is clearly unreliable as a taxonomic criterion, especially in view of the probability, noted above, that the *O. nanum* holotype represents a sub-adult individual. The significance of the second character is uncertain. None the less, in view of the almost complete absence of a skull in the holotype specimen and the lack of adequately detailed descriptions of other *Ophiderpeton* species, it would seem advisable to retain *O. nanum* as a distinct species, at least pending thorough revision of the Ophiderpetontidae.

The possible presence of an interclavicle in *O. nanum* is a feature of some importance. Steen (1931, p. 876) identified two bones in a specimen of *O. amphiuminum* from the Westphalian D of Linton, Ohio, as clavicle and cleithrum, but these were subsequently reinterpreted by Baird (1964) as possibly representing hyoid elements. Most recent workers have concurred in regarding described aistopod species as lacking both limbs and limb girdles. However, Goin and Goin (1971, p. 67) have pointed out that forelimbs are not known for most fossil members of the urodele family Sirenidae, despite their presence in the three extant species of this group. They suggested, therefore, that the Aistopoda may possibly also have possessed vestigial forelimbs which, together with the pectoral girdle, were usually lost prior to fossilization. If the element tentatively identified as an interclavicle in the holotype of *O. nanum* is correctly so interpreted, its presence at least partially confirms the above hypothesis.

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